

A COMPARISON OF NORTHERN AND SOUTHERN FORMS OF *PHIDIPPUS AUDAX* (HENTZ) (ARANEIDA, SALTICIDAE)

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ABSTRACT

Phidippus audax (Hentz) has been considered a single variable species by some taxonomists and two or more distinct species by others. Individual northern and southern specimens, though similar, can usually be distinguished by differences in size and markings evident even to the naked eye. Closer examination, however, failed to reveal consistent differences in morphology between northern and southern populations. Observed behavioral patterns that were compared also failed to show discernible differences. Laboratory cultures of separate and mixed populations were maintained through three generations.

Conversely, inter-geographical cross-matings indicated a degree of incompatibility between the populations. Matings between northern and southern specimens were less successfully achieved than intra-geographical matings. The number of viable young produced by cross-mated females was consistently less than the number produced by females mated to males from their own region. Further, the progeny of cross-bred spiders, when they were mated after maturity, produced even fewer viable young. Such evidence of incompatibility between northern and southern forms may indicate a clinal population.

INTRODUCTION

One of the most commonly seen spiders in the United States is a large black jumping spider that has a prominent white or red patch in the center of the dorsum and other less evident white markings on the carapace and abdomen. Usually it is known as *Phidippus audax* (Hentz), but it has also been recorded as *P. variegatus*, *P. a. bryantae*, and *P. tripunctatus* among other names by various authors. It occurs from Mexico to Canada, and there has been no agreement as to whether it is a variable single species or several. Some of the differences between typical northern and southern specimens are readily evident to the naked eye. A comparison of 44 northern and 35 southern specimens, for example, showed northern females having an average total length of 12.5 mm (range, 10.5-14 mm) compared to an average total length of 14.3 mm (range, 12-18 mm) in southern females. The size of the males showed a similar difference, an average length of 10.6 mm (range, 10-12.5 mm) in northern specimens compared with an average of 12.2 mm (range, 10-14.5 mm) in southern specimens. There was also a considerable individual variation in the quantity of white scales on the carapace and abdomen, hence

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different color patterns. Southern specimens generally were more vividly marked, but no standard regional pattern could be discerned. The shape of the embolus, a characteristic often used taxonomically to separate spider species, was consistently different in northern and southern males, sickle-shaped and pointed in northern specimens and straight and blunt in southern specimens.

MATERIALS AND METHODS

Collection and maintenance of specimens—*Phidippus audax* over-winters as a penultimate or younger instar. In order to have virgin females to work with, immature specimens were collected in January, February and March in Hidalgo and Victoria Counties in south Texas and near Warrensburg, Missouri. In the laboratory they were transferred to transparent plastic containers, 80 × 78 mm, which provided the visibility necessary for observing the spiders' daily behavior. A hole was burned through the lid and covered with tape to facilitate feeding without disturbing the spider. For economy of space and ease of maintenance small spiderlings were kept in short lengths of glass tubing. The reduced living area of the tubing also improved the capability of second and third instar spiderlings to capture live *Drosophila* which were their main diet. (Peck and Whitcomb, 1967)

Satisfactory observation of the courtship behavior required a mating chamber that would provide both adequate room for the spiders to maneuver and good visibility and also afford a means of introducing the male to the female with the least amount of disturbance. Juxtapositioning the clear plastic rearing chambers on a block of styrofoam carved to hold them in place was very efficient. The aggressiveness of the female suggested the placing of a transparent partition between the containers to protect the male until he started courtship. Once the male started signaling, the partition was removed allowing both spiders free access to the common mating chamber (Fig. 1).

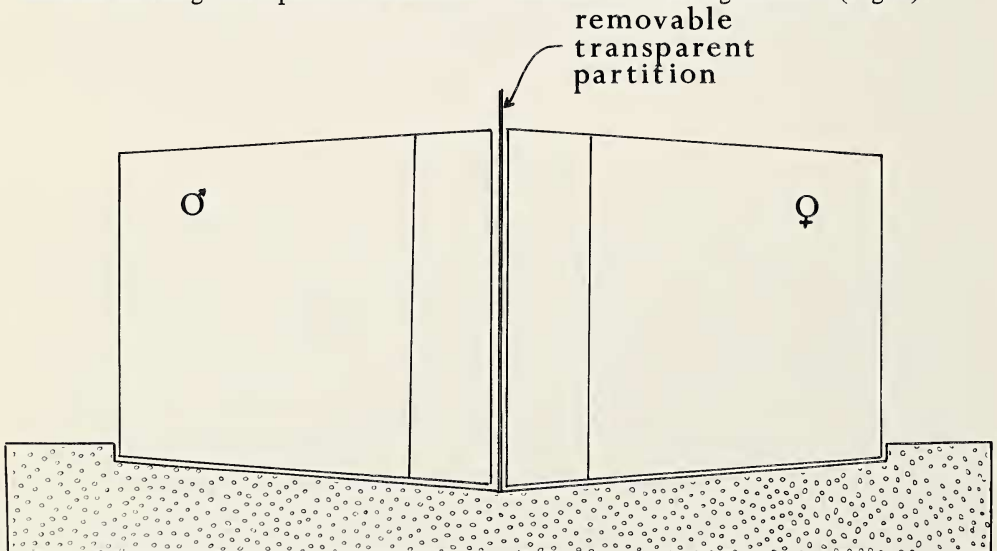


Fig. 1.—Mating chamber for the observation of courtship and copulation.

Vagrant, diurnal *P. audax* are known to feed on a variety of prey (Bailey, 1968), and a variety of food sources was used to supply as natural a diet as possible. During the first

three instars, *Drosophila* sp. was the main diet. When the spiderlings grew larger, almond moths, *Caudra cautella* (Walker) and meal worms, *Tenebrio* sp. were offered regularly. During the summer months, orthopterans, homopterans, and other insects were fed, and cultures of wax worms, *Galleria mellonella* (Linn.), were established to provide a steady supply of prey of an appropriate size.

It seemed necessary to prevent the adult spiders with their acute vision from seeing each other continuously if valid courtship behavior was to be observed later. Hence the individual transparent containers were placed in low boxes and separated by partitions. With 12 containers to a box, handling for daily observations and feeding was simplified and the spiders were kept visually isolated. An enclosed glass cabinet roughly maintained an average relative humidity of 52% or higher, and moistened cotton provided ingestible water in each container. The photoperiod was controlled and gradually increased from 10 to 16 hours at the proper time of the year as recommended for optimal rearing conditions by Miyashita (1968). The temperature remained unchanged at about 80°F.

DISCUSSION AND RESULTS

Various species of *Phidippus* and some other salticids have been extensively studied by a number of researchers (Peckham, 1895; Gerhardt, 1928, 1933; Bristowe, 1926, 1929; Kaston, 1936; Crane, 1949; Bailey, 1968; Wild, 1969; Horner and Starks, 1972), but certain detailed aspects of the bionomics and behavior of *Phidippus audax* that became evident during this study are reported herein for their intrinsic value.

Courtship and mating—The chain of inherited, instinctive actions that forms a fixed behavior pattern such as found in spider courtship has as its links a series of specific releasers that are provided only by the other sex of the same species. A specific action by the male acts as the releaser for a specific response by the female, which, in turn, elicits another response by the male. The patterns are as characteristic of a species as its physiology or its structural features. Hence they may serve as isolating factors that prevent interbreeding between true species.

The courtship pattern of pairs of spiders in which both members had been collected from the northern portion of the studied range was carefully observed and compared with that of pairs from the southern portion of the range. Differences in the patterns, if any, eluded the human observer. Trial matings between northern males and southern females, and the reciprocal, were also attempted and successfully accomplished although some evidences of incompatibility were revealed (Table 1).

Table 1.—Mating northern and southern forms of *Phidippus audax* under laboratory conditions.

Mating pairs	Successful on 1st mating trial	Unsuccessful on 1st mating trial
Northern ♂ × Southern ♀	8	1
Southern ♂ × Southern ♀	2	0
Total intra-geographical trials	10	1
Northern ♂ × Southern ♀	6	9
Southern ♂ × Northern ♀	9	1
Total inter-geographical trials	15	10

When the male and female, each in its own container, were placed on the mating stage, they were generally quite inactive due to having been disturbed. Neither showed signs of seeing the other until one of them moved. If the female saw the male first, she normally began a typical hunting behavior pattern as described by Gardner (1964). That is, she would orient herself toward, pursue, or jump at the male. The male, upon seeing her movement, would begin his courtship signaling by elevating the carapace, raising the first pair of legs at a 45° angle and bending them slightly at the femur-patellar joint. He continued by moving his raised front legs in two jerky motions, drumming his palpi, and moving laterally. Intermittently the male would "pose" holding his elevated legs and palpi motionless. If the male's "epigamic rhythm," as reported by Crane (1949), was at a low tone, he might strike back at the female rather than court. If the male saw the female first, he would orient toward her, watch her quietly, move toward her, or start signaling immediately. The male's signal was normally started when the female made a move in his direction.

The female responded to the male's signaling by raising her body and swaying in his direction when he moved laterally. She might elevate her front legs slightly as she swayed. As the male continued his display he often completely circled the female, gradually closing the distance between them. The female became totally attentive to the male as he approached, lowered her body, retreated slightly, and ultimately allowed the male to touch her with his front legs. If she did not move after several taps, the male mounted, ending courtship and commencing copulation. Although the partition between the containers of the male and female was removed only after the male had signaled and initiated courtship, the female attacked on several occasions. Usually the male escaped without being killed, and in several instances after being attacked a male again initiated courtship and successfully mated. Fig. 2 shows the sequential pattern of courtship.

The mating position is a slight modification of position No. 1 described by Kaston (1948). Insertions of the embolus were made alternately on each side several times. Successful copulation was indicated by rhythmic pulsations by the male shortly after he was in position. A total of 25 successful and 11 unsuccessful mating attempts were observed under laboratory conditions. An average mating lasted for one hour and 18 minutes but the time ranged from 14 minutes to two hours and 48 minutes. The female normally terminated copulation by moving while the male was attempting to change sides. When this occurred the male moved quickly off of the female posteriorly and was typically signaling with raised front legs by the time the female turned to face him. A male usually tried to court the female again but was never observed to succeed.

Table 1 shows the results of mating attempts between pairs from the same geographical area and pairs with one northern and one southern member. Whereas there were successful matings in all combinations, it is interesting to note that although more than 90% of the intra-geographical mating attempts were successful, only 60% of the inter-geographical attempts succeeded. There is a considerable difference in the size of northern and southern specimens and this difference was most readily evident when a northern male was paired with a southern female. Although initially all of the pairings were made by random selection, later combinations of size-compatible mates were tried. It was found that the largest of the northern males in the culture would mate with moderate sized southern females, but the average, smaller northern male when paired with a typically larger southern female could never be made to mate. The progeny that resulted from each of these mating combinations, discussed in the next section, showed some of the same incompatibility that was evident in the mating.

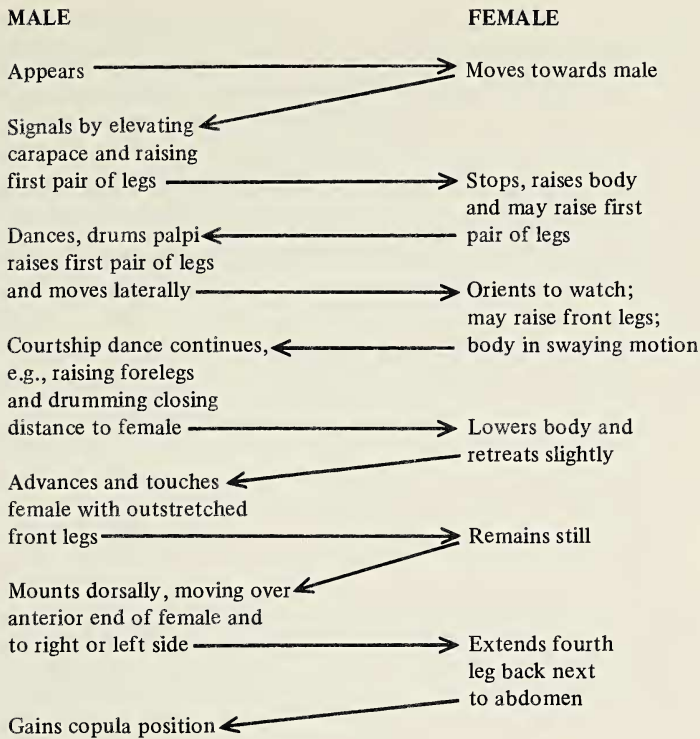


Fig. 2.—Sequential pattern of courtship in *P. audax*.

Progeny—All mating combinations produced viable young, and some of the “hybrid” progeny of inter-geographical matings were reared to maturity, mated, and produced a viable F_2 generation. A noticeable discrepancy in the production of young from the different mating combinations was shown, however. The mean number of egg sacs, of young per egg sac, and of total viable young for each mating combination is shown in Table 2. Southern females produced more egg sacs per individual and averaged a greater number of young per egg sac regardless of the origin of the male with which they were mated. Southern females that were mated with northern males, however, produced only about 65% of the young that were produced by those that were mated with males from

Table 2.—Production of egg sacs, young per egg sac, and total young in each mating combination. The number of females from which means were derived is shown in parentheses.

	N ♂ × N ♀ (8)	S ♂ × N ♀ (7)	S ♂ × S ♀ (8)	N ♂ × S ♀ (6)
Mean number egg sacs	3.5	2.7	4.1	3.5
Mean number of young per egg sac	63.9	41.7	85.5	65.6
Mean number of young per female	224	113	353	230

their own geographical region. Northern females that were mated with southern males, furthermore, produced scarcely 50% of the average production of northern females that were mated with northern males.

Females produced from one to six egg sacs during the productive period, and it has

been noted in spiders generally that each successive oviposition contains fewer eggs (Peck and Whitcomb, 1970; Kaston, 1970). The young that emerged from each of the first four egg sacs produced by several females in all mating combinations were recorded. The mean production for each is tabulated in Table 3. The difference in the production at each oviposition parallels the difference in the total production.

One female from inter-geographically mated parentage, when mature, was mated with a male of southern parentage. She produced 58 viable young in the only egg sac recorded. Two males resulting from inter-geographical matings were mated with females of southern parentage. The latter produced 45 and 54 young in the first and only egg sac

Table 3.—Mean production of young from each of the first four egg sacs in each mating combination. The number of egg sacs from which means were derived is shown in parenthesis.

Egg sac	N ♂ × N ♀	S ♂ × N ♀	S ♂ × S ♀	N ♂ × S ♀
1st	(8) 88.6	(5) 69.8	(7) 125.6	(5) 107.4
2nd	(7) 76.7	(5) 49.8	(7) 115.5	(4) 83.2
3rd	(7) 65.2	(3) 73.6	(7) 83.2	(3) 56.0
4th	(1) 66.0	(2) 35.0	(6) 70.5	(2) 12.5

recorded for each of them. This production is far below the mean number of young from first egg sacs, but whether the reduced number of young in these cases could be attributed to the mixed parentage involved or to two generations of life in the laboratory is an unanswered question.

Development—The total progeny from 29 egg sacs was observed daily to record morphological and behavioral details in the developing spiderlings throughout postembryonal development in an effort to discern any variability between the young of the southern and northern forms and their “hybrids.” Although none could be detected, again the detailed observation that was required revealed certain developmental aspects that may be intrinsically of value.

Oviposition occurred inside a typical resting cell, an ovate, dome-shaped structure of silk that measured about 45 × 30 × 10 mm, varying somewhat with the size of the female. Guy lines attached to the outer surface apparently provide structural stability, and the cells were open at both ends. Preparation for oviposition by the gravid female began with the construction of a silk platform inside the resting cell. The egg mass was deposited on this disc-like platform in a viscous mound that measured 4-10 mm in diameter depending upon the number of eggs it contained. When oviposition was complete, the female covered the mass by passing silk lines back and forth over it and attached them to each side of the base until a complete, lenticular capsule was formed.

To observe egg development, it was necessary to remove one side of the egg sac, which is rather easily done along the lateral seam. One layer of eggs is thus exposed nested in the saucer-like remains of the egg sac. In this form the eggs were then placed in a watch glass which was in turn placed in another closed container with water to maintain a high humidity as described by Holm (1940).

The color of the eggs varied from pale yellow, which was most common, to light green. The same female was found to produce both yellow and green eggs at different ovipositions although all eggs in any one egg mass were homogeneously colored. Egg diameters ranged from 1.13 to 1.33 mm. The first sign of change occurred five to seven

days after oviposition when the tightly packed eggs began to expand and automatically dislodge from the mass due to a bulging that changed the egg shape from spherical to ovate. Nine to 12 days after oviposition a faint outline of the embryos' legs, chelicerae, carapace, and abdomen could be seen through the chorion. Egg teeth could be detected as two dark spots, one at the base of each chelicera.

Eclosion began with slight pulsations along the lateral areas of the outlined carapace about two days after this outline was visible. The chorion began to part over the egg tooth and split posteriorly along a line following the base of the carapace. Over a period of about an hour it slipped off the carapace and abdomen, passed ventrally over the chelicerae and legs, and remained attached in a wad at the spinnerets. Following the suggestion of Galiano (1969) for observing egg membranes, an ink spot was applied on the vitelline membrane that still encompassed the embryo. Although the membrane itself was difficult to see, this ink spot and the egg teeth which are on the vitelline membrane could be followed in their movement when this membrane was shed. After this membrane is shed the spiderling's abdomen is still positioned at right angles to the carapace and the legs are pressed, fully extended, length-wise along the body as in the previous stage because the spiderling is still encased in a third membrane. Since it was all but impossible to see this membrane, a second ink spot applied at the point vacated by the previous one was an effective means of observing the progress of its sloughing. The shedding of this third membrane required several hours, but at its completion the body setae began to stand erect, and the spiderling's abdomen assumed the same plane as the carapace. Although now free from any enclosing membranes, the spiderling lay immobile on its side or back with its legs extended straight out from the body. The only movement evident was a slow flexing of the tarsi.

The newly emerged spiderling was essentially the same color as the egg. Within eight to ten hours the integument of the carapace and abdomen began to darken. Eye spots were visible but remained colorless except for a dark, heavily pigmented border. They appeared to be light sensitive as leg movements increased noticeably when a light beam was directed on the spiderlings. The spinnerets were present but presumably not functional (Vachon, 1958). The chelicerae and fangs were separately articulated and probably functional to some extent. Previously, Kaston (1948) and others believed that the spiderling never fed at this stage but depended wholly upon vitelline reserves. However, it has since been noted, reported by Peck and Whitcomb (1970), Galiano (1969), Kaston (1970) and Schick (1972) that some of these newly hatched spiderlings develop swollen abdomens typical of older spiders after they have ingested a substantial quantity of food. These spiderlings were almost always found near a dead, deflated, embryonal spiderling that had not completed eclosion and some have been observed feeding. A few spiderlings at this stage in this study were also observed feeding on unclosed eggs. There was no evidence of predation upon fully eclosed spiderling.

For the first two days after eclosion movement was principally limited to desultory flexing of the legs although an increasing degree of coordination was evident during this time. By the end of the two days the spiderling was able to right itself and move feebly from place to place. Their mobility on the silk of the egg case was much better than it was on the smooth surface of the container where they could scarcely maneuver at all. Since they would still be enclosed in the egg sac under normal conditions their mobility needs at this time are very slight.

The first true molt under natural conditions occurs inside the egg sac about ten days after eclosion, and the second instar spiderling remains in the egg sac for four to seven

days before emerging. Spiderlings that hatched from egg sacs that had been opened for observation remained congregated on the egg sac silk for several days in this same way before scattering. Kaston (1965) believed that this voluntary scattering is a result of changes in their tropistic behavior that occur at this time.

Morphological changes in immature spiderlings—The second instar spiderlings were fully equipped to fend for themselves away from the egg sac. Their evident awareness of their surroundings and their ability to stalk and capture prey indicated functional eyes. Better coordination and claw tufts, which were lacking in the previous stage,

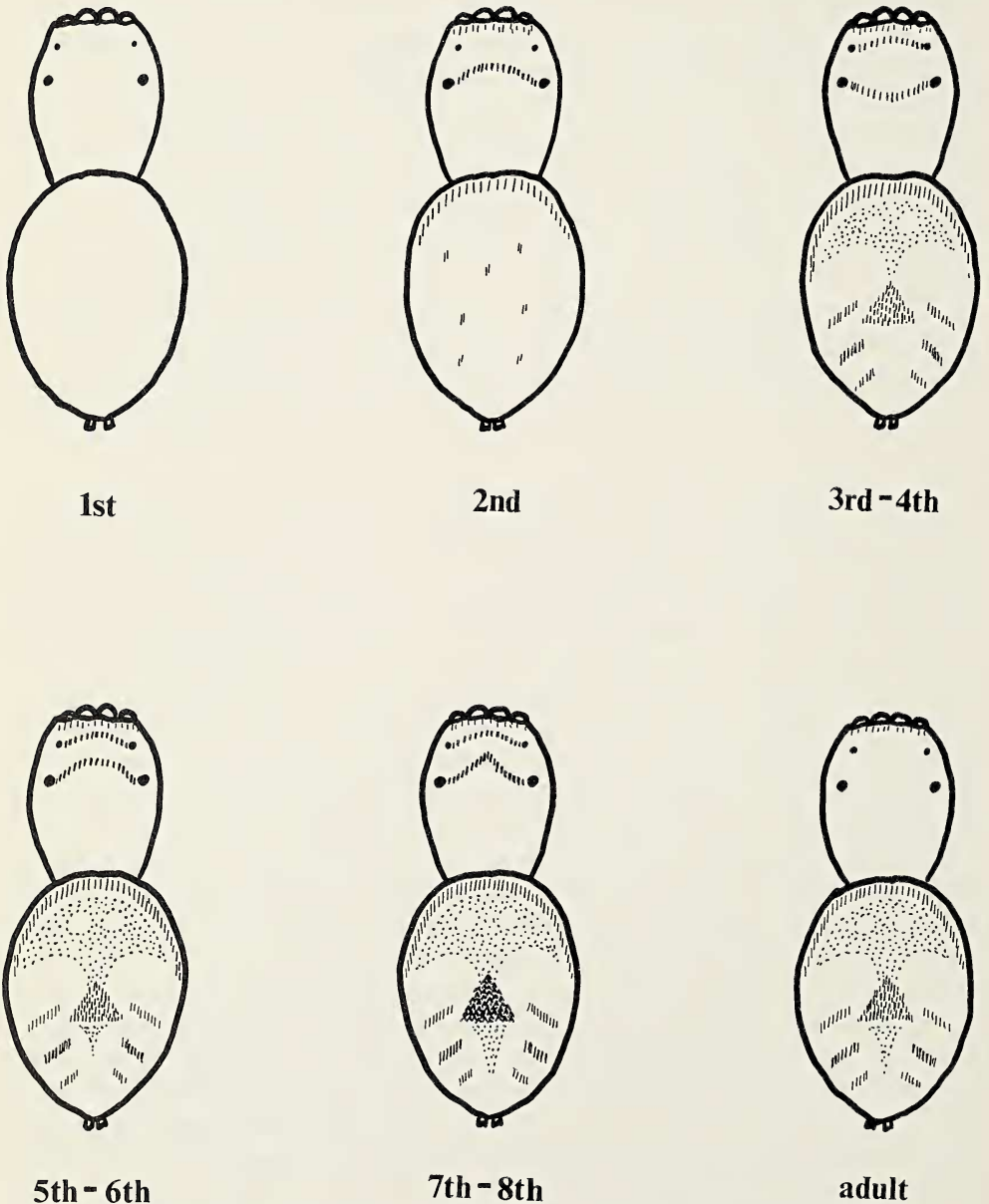


Fig. 3.—Progressive changes in color patterns typical of the developmental stadia.

allowed them to move on any surface and in any plane. That the spinnerets were functional was obvious from the myriad drag lines that began to cover the container and the small resting cells that were built.

Superficial, sequential, changes in the pattern of color scales, and the pigmentation of the integument of the carapace, abdomen, and legs became evident, but they were apparently uniform in all spiderlings regardless of parentage. The features noted hereafter were typical progressive changes in all the spiderlings reared. The first instar darkened from the yolk color of the egg at eclosion to jet black by the time of the first molt. Unlike succeeding instars, these spiderlings lacked color scales altogether, but the banded color pattern of the integument of the legs was much the same as that of other immature instars. This banded appearance resulted from the contrast of the black coxae, trochanters, and femora with the reddish brown patellae. The tibiae, metatarsi and tarsi each are reddish brown proximally and black distally. This pattern remained unchanged until maturity except that the bands became more distinct with age.

Other changes that occurred in the color patterns of the carapace and abdomen hereafter described, were due to an increasing quantity of scales that appeared at each successive instar. The black second instar spiderlings had a few white scales scattered sparingly on the carapace, around the large anterior median eyes, and in a band that crossed the carapace between the third eye row. The abdomen was marked with a faint dorso-anterior band of white scales, and a few others were scattered over the dorsum.

A considerable change in both the amount of scales and their pattern was seen in the third instar. The clypeus and the area between the eyes of the anterior eye row were densely covered with yellowish or off-white scales. A recurved band of scales of this same color crossed the carapace between the PME (second eye row) and a procurved band crossed between the PLE (third eye row). The anterior band of scales wore off toward the end of the instar due to the spiderling's moving about and brushing this high point of the carapace against the resting cells as it entered and left them. The posterior band was not affected, and the result was that of leaving the carapace unscaled and black in the center just prior to the molt.

The black abdomen of the third instar was marked with a distinct dorso-anterior band of white scales that extended posteriorly along the sides of the abdomen about one third of its length. Each side of the cardiac area was covered with some rather inconspicuous dark metallic scales, and posterior to them, and almost in the center of the dorsum, there was a triangular-shaped patch of white scales. To each side of this spot and separate from it were small bars of white scales extending laterally, and posterior to them and to the white patch were two more pairs of white bars that angled posteriorly.

Later instars displayed only slight variations of this same pattern. A greater abundance of metallic scales forming a more dense pattern occurred in the fourth instar. The fifth instar showed a slight posterior curve in the band of scales between the PLE which became more pronounced in the sixth instar and darkened to a reddish-yellow. In the sixth instar the metallic scales on the abdomen extended more posteriorly also to an area posterior to the central white patch. This white patch, in one instance, became red in this instar as well.

The color change of the abdominal markings from white to red was apparently characteristic of the antepenultimate and the penultimate instars. Thirty two percent of the spiderlings showed the change in their seventh instar, 35% in the eighth, and 20% in the ninth. The change occurred in spiderlings of both sexes, and all regained white markings as mature males or females. Fig. 3 graphically outlines the sequence of the changes in the

pattern as spiderlings develop.

Growth rate—Neither males or females attained maturity in a standard number of instars, and no pattern of difference in growth rate between northern and southern forms or in the progeny of inter-geographical matings was evident in 31 specimens whose entire life cycle was recorded. Table 4 illustrates the instar of maturity of individuals from nine broods. Males seem typically to mature in the eighth and ninth instar and females in the tenth, but a considerable number completed their development earlier or later.

Table 4.—Maturity instar of males and females from different mating combinations.

Parentage	8th Instar		9th Instar		10th Instar	
	Male	Female	Male	Female	Male	Female
S ♂ × S ♀ (5 broods)	0	0	4	2	0	5
N ♂ × N ♀ (1 brood)	0	1	0	0	0	0
S ♂ × N ♀ (1 brood)	3	0	2	0	0	6
N ♂ × S ♀ (1 brood)	0	0	0	0	0	6

The total number of days required to reach maturity varied greatly but no pattern relative to parentage could be considered conclusive. Four males from three broods of S ♂ × S ♀ parentage required a mean number of 244 days to reach maturity. However, five males from a single brood of S ♂ × N ♀ parentage reached maturity in a mean of 174 days, and all reached maturity within a period of 15 days. On the other hand six females from the same egg mass just cited (of S ♂ × N ♀ parentage) matured in a mean of 273 days and all within 30 days of each other while six females from the three broods mentioned earlier (S ♂ × S ♀ parentage) required a mean of only 256 days to reach maturity and the span between the earliest and the latest to mature was 101 days.

Both males and females displayed similar patterns in instar length for the first four instars. The mean duration of the instars for females was 10, 11.7, 14.8, and 17.3 days respectively compared with 10, 10.8, 13, and 15 days respectively for males. Deviation from these means did not exceed four days in these instars. Beginning with the fifth instar, however, the close uniformity of instar durations was lost, and deviation from the mean duration was as much as 23 days. The last two immature stadia were the longest regardless of sex or the instar of maturity. An inherent "diapause" of this sort may be correlated with the habit of these spiders to hibernate during the winter months in these later instars.

A rise in the mortality rate at the completion of the fifth instar was also evident. High survival rates of 100, 98, 96, and 96% were recorded for the first through the fourth instars. Eighty percent survived the fifth instar, but the rate dropped to 40% in the sixth and remained low thereafter. No external change in the environmental condition could be attributed to causing this change in mortality. And because it occurred in all broods, it, along with the onset of much less uniformity in the stadia duration, may indicate that this is a critical stage of growth that may be correlated with physical changes in the spider.

CONCLUSION

Slight morphological differences in the embolus, differing patterns of color scales, and a considerable variation in size, all traditionally bases for separating spider species taxonomically, and ones which have been used previously to separate the northern and

southern forms of *Phidippus audax* (Hentz) as different species were confirmed in this study. It was shown, however, that these differences are not sufficient for reproductive isolation in this spider since viable young resulted from all mating combinations. On the other hand, the reproductive efficiency of inter-geographically mated pairs was noticeably reduced indicating the possibility of some degree of genetic incompatibility. There is no evidence that the northern and southern populations are or have been geographically isolated, and they doubtless represent a single, but widely dispersed gene pool with little interaction between individuals of the geographic extremes.

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